MODELING HABITAT SUITABILITY AND CONNECTIVITY OF GRAY WOLF (*CANIS LUPUS*) POPULATIONS IN THE PACIFIC NORTHWEST

By

Jacob I. Mesler

A Thesis Presented to
The Faculty of Humboldt State University
In Partial Fulfillment of the Requirements for the Degree
Master of Science in Natural Resources: Wildlife

Committee Membership
Dr. Micaela Szykman Gunther, Committee Chair
Dr. Tim Bean, Committee Member
Dr. Dan Barton, Committee Member
Dr. Yvonne Everett, Graduate Coordinator

July 2015

ABSTRACT

MODELING HABITAT SUITABILITY AND CONNECTIVITY OF GRAY WOLF (*CANIS LUPUS*) POPULATIONS IN THE PACIFIC NORTHWEST

Jacob I. Mesler

Since extirpation from almost the entirety of the United States in the early 20th century, gray wolves have begun to reestablish populations across their historic range. After reintroduction of wolves into the greater Yellowstone area in 1995, wolves have expanded their range to include a large number of western states. Rising to a population size of almost 1700 wolves in the Northern Rocky Mountains, wolves have expanded their initial range to move into other regions to the North and west of the reintroduction zone. As wolves continue to disperse into new areas it is important to identify likely areas of pack establishment and dispersal pathways. This study used global positioning system (GPS) collared wolves to identify such areas in the Pacific Northwest. The spatial modeling program Maxent was used to identify areas of high quality wolf habitat throughout the study area of Washington, Oregon and California, with distinction made between wolves within packs and those conducting long distance dispersal. Wolves within packs selected habitat based on an ungulate density index, land cover type, and slope while dispersing wolves selected habitat based on an ungulate density index and anthropogenic impact. Using this information, possible dispersal corridors were identified using least cost path analysis. These techniques were used to identify potential areas of future wolf dispersal and expansion, with possibility of future conflict with people. Identifying these key areas can assist managers in planning and preparation for wolf immigration into their regions.

ACKNOWLEGEMENTS

I would like to thank my advisor, Dr. Micaela Szykman Gunther, and my committee members Dr. Tim Bean and Dr. Dan Barton for their support and guidance. I would also like to thank the Washington, Oregon, and California Departments of Fish and Wildlife, as well as the Idaho Department of Fish and Game for providing wolf GPS data necessary for this project. Thank you also to Brian Kertson, Karen Kovacs, and Darren Clark for reviewing my thesis and providing comments. I would also like to thank Emily Cate for her support, including assistance with analysis and helpful commentary throughout the process.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Large carnivores in North America have been consistently persecuted since the arrival of European settlers. This persecution led to a sharp decline in predator populations throughout the continent by the beginning of the 20th century (Kellert et al. 1995). However, in recent years greater protections have been placed on these species, as societal attitudes towards at-risk species change and research uncovers the ecological importance of these animals (Wilmers et al. 2003; Musiani and Paquet 2004). With this increased protection, many large carnivores have begun to recolonize portions of their historic ranges. Cougars (*Felis concolor*), once restricted to only a portion of their western range, have begun to expand eastward into the mid-west (LaRue and Nielson 2008). Grizzly bears (*Ursus arctos*) also show signs of range expansion in the Northern Cascades of Washington, and a trend of population increases across their range (WDFW 2012).

In the absence of human persecution, large carnivore populations have expanded primarily as a result of foraging behavioral-plasticity and dispersal behavior. Large carnivores are often able to obtain food from multiple sources, depending on prey availability (Weaver et al. 1996). This flexibility in prey use can allow carnivores to inhabit regions disturbed by humans. Additionally, the establishment of large defended territories often requires large carnivores to disperse far from their natal ranges (Weaver et al. 1996). Flexibility in prey source and high mobility allow carnivores to travel through habitat that would otherwise be unable to support them in the search for unoccupied territory in which to ultimately settle.

After suffering decades of purposeful eradication, the gray wolf (*Canis lupus*) is also making a comeback in the northwestern United States. However, unlike other large carnivores in North America, wolf range expansion was enabled by reintroduction efforts. After the listing of wolves as endangered on the endangered species list in 1974, wolf populations were considered to be within either the Great Lakes recovery zone or the Northern Rocky Mountain recovery zones. The majority of wolf range expansion has occurred within the Northern Rocky Mountain recovery zone, aided by reintroduction efforts in 1995 and 1996.

Gray wolf management within the Rocky Mountains has surpassed recovery goals in all three U.S. Fish and Wildlife Service recovery areas in Central Idaho, North Western Montana, and the Greater Yellowstone Area (Wyoming) by maintaining at least 10 breeding pairs in each recovery area for a minimum of 3 consecutive years (USFW 1987; Gude et al. 2012). In addition, wolves have begun to disperse to a lesser degree into the Pacific Northwest, including Washington and Oregon, with occasional forays into northern California. Despite the legalization of regulated harvest following the delisting of wolves in the Northern Rocky Mountain recovery areas, population estimates have continued to predict an upward trend (Gude et al. 2012).

The impact of these wolves has long been controversial due to conflicts with humans, such as the killing of livestock and pets. However, research has begun to show the positive environmental impact of these animals. For example, the presence of wolves in Yellowstone National Park has been suggested to have reduced the overgrazing of elk (*Cervus elaphus*), especially in riparian ecosystems (Ripple et al. 2001). This has led to a measurable increase in western tree species such as the quaking aspen (*Populus tremuloides*; Ripple et al. 2001). The reintroduction of wolves into Yellowstone National Park has also been linked to a recovery of small mammalian prey species as a result of competitive interactions between wolves and coyotes (*Canis latrans*; Miller et al. 2012). Wolf kills have also been suggested to provide a stable food source for scavengers during winter months in Yellowstone National Park (Wilmers et al. 2003).

In the century prior to their extirpation and subsequent reintroduction, wolves were associated with wilderness and were believed to naturally colonize remote habitat (Mladenoff et al. 2009). However, as wolf recovery has progressed over recent decades, it has become apparent that the reduced ability of wolves to colonize habitat in close proximity to humans is due to human-related conflict (Mladenoff et al. 2009). As a result of habitat movement restrictions due to such conflicts, wolves are expected to be most restricted by prey abundance (Mladenoff et al. 2009). The presence of large ungulate populations, as well as the existence of large areas of low human density in un-colonized areas of the Pacific Northwest, indicate likely future expansion of wolves throughout the region.

The basic social structure of the gray wolf is a pack, generally consisting of a single socially dominant breeding pair, accompanied by multiple litters of offspring (Mech and Boitani 2007). Living in a pack structure is believed to be evolutionarily advantageous, not necessarily due to their ability to hunt larger prey or increase hunting efficiency, but rather the increased supply of food available to younger wolves from pack kills (Mech and Boitani 2007). This subsidizing of young wolves provides support for pups as they grow to sexual maturity and to age of dispersal (Mech and Boitani 2007).

Both male and female wolves tend to disperse from their natal packs at approximately one to two years of age (Mech and Boitani 2007). These newly dispersed wolves form new packs by budding, splitting, usurping, and long distance dispersal. In budding, a single wolf disperses and establishes a territory adjacent to their natal territory, while packs that split usually result in several pack members dispersing to form a new territory. In usurping, a younger wolf will replace a dominant breeding individual, through combat or a natural death, usually resulting in a daughter replacing a mother as the alpha female. Distant dispersal differs from these other pack formation methods in that it entirely removes a wolf from its natal and surrounding habitat. In long distance dispersal an individual of either sex disperses enormous distances generally in a single direction. This directional dispersal allows wolves to maximize distance travelled and facilitates colonization of uninhabited areas. Dispersing wolves are then able to form a new pack with a member of the opposite sex in an area previously uninhabited by wolves (Mech and Boitani 2007)

Wolves eat a variety of prey items, but by far the most common prey items consumed are ungulates. Throughout their worldwide range, wolf populations vary greatly on the primary ungulate prey species, but often a wolf population will specialize their hunting strategy to prey upon the most available ungulate species. For example, in Wood Buffalo National Park in Canada, wolves specialize on bison (*Bos bison*), while wolves on Isle Royal in Michigan famously specialize on moose (*Alces alces*) (Peterson 1975; Carbyn et al. 1993). In the western United States, wolves primarily prey upon elk where present as well as secondarily preying upon deer (*Odocoileus sp.)*. Where elk are less abundant or completely absent, wolves are observed to prey primarily on deer. These patterns change slightly in summer when wolf packs are much less structured and individual wolves often forage alone. During the summer, wolves have been observed to eat a vast array of prey items including rabbits, carrion, rodents, human trash, and beaver (*Castor canadensis*; Stephenson and Johnson 1973; Voigt et al. 1976; Marquard-Peterson 1988). However, the primary prey source remains young ungulates even when availability of other prey sources may increase (Stephenson and Johnson 1973; Mech and Boitani 2007).

The historic distribution of the gray wolf once included the entirety of the Pacific Northwest including Washington, Oregon, and Northern California (Rutledge et al. 2010). As wolves return to the Pacific Northwest via expansion from the Rocky Mountain and Canadian populations, it is essential to understand not only what habitat is suitable for wolves to colonize, but more importantly, to determine regions which allow for enough connectivity to accommodate wolf expansion, without causing conflicts with humans. This is specifically important for large carnivores with naturally long-distance dispersal and relatively low population densities in order to increase gene flow and to prevent density pressures which may result in increased human conflict (Carroll et al. 2011). The ability to predict areas of wolf expansion will allow managers to prepare resident human populations to reduce future conflicts.

The controversial nature of expanding wolf populations has left the public split on its perception of the prospect of increasing wolf numbers in the Pacific Northwest. Primary concerns of the public in Washington are livestock depredation, simply too many wolves, and danger to humans (Responsive Management 2014). In areas with high levels of agriculture and lower population densities, residents tend to be against wolf expansion (Responsive Management 2014). This is compared to the western portions of these states where human populations are more urbanized and public opinion is primarily in support of wolf expansion (Responsive Management 2014).

A major concern of modern conservation efforts is identifying habitat deemed appropriate and of high quality for a species to occupy. However, despite its importance in management plans, the term habitat is often loosely defined (Hall et al. 1997). Within this study habitat will be defined as “an area with the combination of resources (such as food, cover, water) and the environmental conditions (temperature, precipitation, presence or absence of predators and competitors) that promotes occupancy by individuals of a given species (or population) and allows those individuals to survive and reproduce” (Morrison et al. 2012). By understanding how animals select habitat and move within it we are able to address the issue of selecting areas for management and protection.

Habitat suitability models are powerful tools in the field of ecology and wildlife management due to results that can be highly informative with respect to species habitat requirements (Hirzel et al. 2001). Oftentimes, when models are created, researchers lump all individual locations together regardless of the animal’s life history. For wolves, the distinction between the habitat requirements of dispersing individuals as compared to wolves belonging to packs residing within a territorial home range is essential for predicting dispersal patterns and areas where packs may successfully persist (Mech et al. 1995; Merrill and Mech 2000). This is particularly relevant to wolves that are reported to travel through otherwise unsuitable habitat while conducting long-distance dispersal (Mech et al. 1995; Merrill and Mech 2000). This distinction is key to understanding habitat selection of expanding populations such as in the Pacific Northwest. Specifically this will allow for the prediction of habitat wolves may use while dispersing to aid in an understanding of habitat connectivity.

I quantified wolf habitat use and landscape connectivity in Washington, Oregon, and California to identify suitable habitat that is likely to support wolf populations and allow for wolf dispersal. By understanding how dispersing wolves move across the landscape we can better predict where new wolf populations may appear. This information can be used to assign observational effort more effectively while surveying for the formation of new wolf packs. Also, pack-specific habitat suitability models will allow for more accurate predictions of home range selection by wolves across their expanding range.

STUDY AREA

The area of interest for this study comprised the entirety of Washington, Oregon, and California (Figure 1). Due to the recent immigration of wolves into California, data used for modeling purposes was restricted to above I-80. This was deemed a suitable boundary for available habitat as habitat below this boundary is unlikely to be inhabited by wolves due to dispersal limitations rather than avoidance. Due to the vast size of these states, habitat characteristics vary dramatically across the study area. In all, the area comprises 863,823 km^2 and varies in elevation from sea level to the highest point in the contiguous United States at Mount Whitney (4421 m).

In Washington and Oregon, coastal habitat is predominantly dominated by lowland conifer-hardwood forest except in the Olympic peninsula (Waring and Franklin 2003). In Washington State's Olympic peninsula, elevations rise to almost 2438 m and vegetation types vary greatly with elevation. Temperatures are relatively mild across the coastal region with precipitation ranging 89-381 cm (Schermerhorn 1967). Elevations within the coastal region range from sea level to approximately 609 m (Johnson and O'Neil 2001). The central regions of Oregon and Washington include the Cascade mountain range, which is dominated by mixed conifer forests, including primarily Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*; Waring and Franklin 2003). The Cascade Mountains are known for being extremely steep and jagged

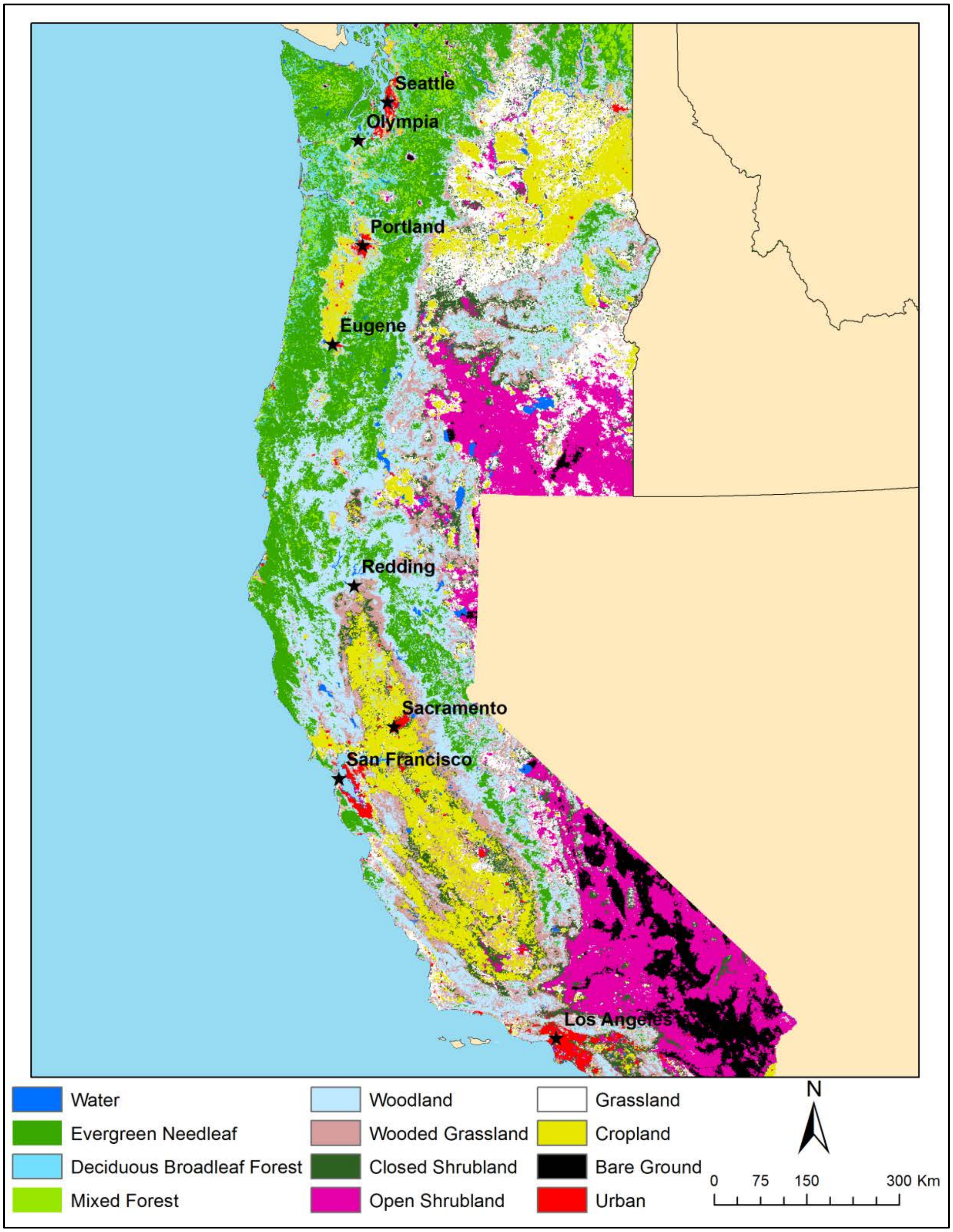


Figure 1. Land cover types based on University of Maryland land cover classification for the study area. Map projected using NAD 83 UTM zone 11N.

and rise to 4391 m at Mount Rainier. East of the Cascades in Washington and Oregon, the terrain becomes primarily shrubland and high desert (Johnson and O'Neil 2001). Primary areas of anthropogenic presence include the Puget Trough from Olympia to Everett (WA), Spokane (WA), the greater Vancouver (WA) and Portland (OR) metro complex, the Willamette Valley in western Oregon, and large amounts of agricultural disturbance in northeastern Oregon, and the majority of southeastern Washington (Johnson and O'Neil 2001).

California is very similar to Oregon and Washington in the northern portions of the state, however southern portions vary greatly. Northwest coastal California is primarily similar to Washington and Oregon coastal environments and is comprised mostly of coniferous forest (USFS 2007). Northeastern California is also similar to southeastern Oregon as most land area is dominated by shrubland habitat (USFS 2007). The Sierra Nevada mountain range is found in north eastern California and continues the majority of the way to southern California (USFS 2007). The center of the state has extremely dense agriculture and pockets of urbanization (USFS 2007). South of the Sierras, the terrain becomes arid and primarily desert (USFS 2007). To the southwest is the Los Angeles and San Diego urban area and to the southeast is the Mojave Desert (USFS 2007).

METHODS

Wolf Location Data

Wolf location data were provided from the initiation of monitoring in these regions, which began in 2009, by the Oregon and Washington Departments of Fish and Wildlife. Wolves in groups of 2 or more adults were considered packs, while those in groups with at least one male and one female that successfully bred, and produced at least two pups that survived to the end of the year, were considered a breeding pair. All packs used in this study were believed to have had at least one male and one female wolf. As of December 2013, the wolf population has grown to 52 individuals in 13 packs (with 5 breeding pairs) in Washington and 64 individuals in 8 packs (with 4 breeding pairs) in Oregon (ODFW 2010; Becker et al. 2013). There are currently no wolves known to be residing in California. Only packs with sufficient data for calculating home ranges were included from 2013, resulting in the use of 6 Washington and 7 Oregon wolf packs (Figure 2). Wolf packs were limited to those present between 1 January and 31 December 2013, to prevent autocorrelation resulting from small movements in wolf territory across years.

The Washington Department of Fish and Wildlife provided GPS collar locations for 18 collared wolves across their 6 packs used here. The Oregon Department of Fish and Game provided 95% Minimum Convex Polygon home ranges for all 7 of their established wolf packs used in this study. Wolves also dispersed from Washington and

Figure 2. Gray wolf pack home ranges created using 95% minimum convex polygons for packs present in 2013 and used for modeling (N=6 WA, 7 OR). Map projected using NAD 83 UTM zone 11N.

Oregon and traveled to other states including Idaho and California as well as into British Columbia. For dispersing wolves, all available data were used, from 11 August 2009 to 5 August 2014, in order to maximize the number of disperser locations available for analysis. Data were available for 10 Oregon and 5 Washington GPS collared wolves that dispersed.

Data for environmental and anthropogenic variables included in models were obtained using free online sources (Table 1). Variables considered for modeling were informed by previous modeling efforts (Larsen and Ripple 2006; Oakleaf et al. 2006; Milakovic et al. 2011). To maintain model parsimony, only variables determined to have likely biological impact and with perceived low correlation to other variables were included. Variables included in model selection were an ungulate index, human footprint, land cover, slope, and minimum annual temperature (Table 1). Environmental variables considered but not modeled included annual precipitation, normalized difference vegetation index, distance to water source, and elevation. These were not included in modeling runs due to their perceived high correlation primarily with land cover type and their expected lack of impact on wolf ecology (Mech and Boitani 2007).

An index for ungulate density was created using total harvest reports from each state, as well as British Columbia, at the lowest possible geographic scale (Oakleaf et al. 2006). This measure was determined appropriate as harvest has been shown to correlate strongly with elk and deer density estimates (Oakleaf et al. 2006). This method was also selected over using individual game management unit (GMU) density estimates due to inconsistent data availability and differing estimation methods between states and Canada

Table 1. Sources of environmental and anthropogenic variables used to construct gray wolf habitat suitability model in Maxent.

Variable	Source	Unit
Ungulate index	State Departments of Fish and Wildlife harvest reports and British Columbia Ministry of Forests, Lands, and Natural Resource Operations	Game Management Unit
Human footprint	NASA's Earth Observing System Data and Information System	1 kilometer
Land cover	USGS Land Cover Institute Facility	1 kilometer
Slope	USGS Earth Explorer	1 kilometer

(Oakleaf et al. 2006). However, this method cannot be considered a surrogate for ungulate density; rather it is considered an index of ungulate abundance and will be presented hereafter as the ungulate index. Areas without available harvest records, such as national parks and tribal lands, were calculated by averaging surrounding GMUs (Oakleaf et al. 2006). Mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and elk were included in the harvest layer. To address the biomass difference between deer and elk, species harvest numbers for elk were multiplied by 3 (Larsen and Ripple 2006). Other food sources were not included as insufficient data were available and these prey types make up a relatively small proportion of wolf diets in this region (Bangs et al. 1998; Metz et al. 2012). Livestock densities were not included due to likely correlation with land cover type and the fact that livestock depredation represents a small proportion of wolf prey (Capitani et al. 2004; Chavez and Gese 2005).

To address anthropogenic impact across the entire study area in a uniform and complete way, a human footprint layer was used. These data consisted of a compilation of several anthropogenic variables including: human population density, human land use type, and infrastructure (SEDAC 2005). Data were combined into a single layer at 1 km resolution (SEDAC 2005).

Habitat land cover was considered to be a likely selection cue for wolves as it is has strong influence over prey availability and movement costs (Oakleaf et al. 2006; Mech and Boitani 2007). This data set classified all 1-km pixels as one of 13 different land cover types. Possible land cover types included water, evergreen needleleaf forest, evergreen broadleaf forest, deciduous needleleaf forest, deciduous broadleaf forest, mixed forest, woodland, wooded grassland, closed shrubland, open shrubland, grassland, cropland, bare ground, and urban (Hansen et al. 1998).

Slope is likely an important environmental variable that may incur cost to wolf movement and alter other environmental conditions such as vegetation cover (Singleton et al. 2002). As a result, slope was considered a variable for habitat suitability modeling. Due to the large study area considered in this study, spatial slope data were only available at a 1-km resolution. Wolves react to their landscape at a much finer scale than 1 km; however, due to their high mobility, it is likely that small scale elevation changes are less important to wolves than large scale elevation changes. Therefore a 1-km digital elevation model (DEM) was utilized. Slope is measured as the change in elevation from the center of a 1-km^2 pixel to an adjacent cell of the same size. This reduces accuracy of small elevation changes such as a creek beds, but may more accurately address environmental cues that wolves are actually selecting such as hill sides. Also, the intent of this study was to find possible corridors through which wolves are more likely to disperse, which does not require a higher resolution slope layer.

Home Range Identification

I delineated wolf pack home ranges using 95% minimum convex polygons (MCP), as this was the form in which the location data were provided by the Oregon Department of Fish and Wildlife. MCPs were created using GPS location data from collared wolves resident in packs using the statistical program R (R Version 1.5). MCPs were also created for the packs present in Washington State, using the same definition of disperser to identify wolves that would be omitted from the pack analyses. To obtain location points within these home ranges for use in Maxent, 25 random points were created within each MCP. This number was selected as it was considered to provide enough points to properly cover the home ranges, while not leading to over fitting (Pearson et al. 2007). We also identified wolf pack home ranges with the traditionally used fixed kernel method for all Washington location data due to the ability of this method to allow calculations of home ranges that more accurately depict proportion of use (Börger et al. 2006). This method for estimating home ranges was used to allow for comparison between the traditional statistically-based method and the results of the non-statistical MCP home ranges.

As wolf re-colonization of the Pacific Northwest is relatively recent, areas not inhabited by wolves cannot be identified as unsuitable locations (Phillips et al. 2014). As a result, wolf location data were considered presence-only locations, indicating that areas that wolves do not currently inhabit have not necessarily been selected against (Phillips et al. 2014). To address the lack of true absence data, background points were selected randomly throughout the non-inhabited area, identified using default Maxent settings (Phillips et al. 2014).

Wolves that were considered to have dispersed during the study period were not included in the formation of pack home ranges. Wolf dispersers were defined as individuals that permanently moved away from their natal home ranges (Boyd and Pletscher 1999). However, wolves do not disperse at a single point in time; rather they perform exploratory forays of gradually increasing distance from the center of their pack home range leading up to a final dispersal event (Mech and Boitani 2007). Disperser points were selected using all location points from individual wolves that did not overlap the MCP home ranges.

Habitat Suitability Modeling

The program Maxent was used for all modeling due to its ability to accurately predict species population distributions with small sample sizes and presence-only data (MAXENT version 3.3.3; Elith et al. 2011). Maxent uses a maximum entropy and machine-learning approach to model species population distributions spatially and performs better than traditional regression-based resource selection function when using presence-only data (Elith et al. 2006; Gibson et al. 2007). To determine the validity of using random MCP points as pack location data, we compared the kernel identified home ranges to those identified using MCPs for Washington wolf packs. Every combination of variables was run in Maxent for both GPS locations within kernel identified home ranges and the MCP-identified random locations. This resulted in the formation of 26 possible habitat suitability models for both kernel and MCP identified wolf packs. All model combinations were run in Maxent using five replicates and a regularization parameter of 3. Multiple replicates were run to allow for the use of cross-validation for model-validation and calculation of modeling uncertainty. In Maxent cross-validation using 5 replicates, location data are randomly separated into 5 equal groupings called “folds” (Merow et al. 2013). As the model replicates, a different fold is withheld from model creation each iteration. This withheld fold is instead compared to the predictive model as a method for evaluating the precision of the model (Merow et al. 2013). These models are then averaged to create a single predictive model. Standard deviation between these models was then calculated to allow for estimation of model precision. The regularization parameter value was chosen to prevent over fitting of the models (Dudik et al. 2004; Phillips and Dudik 2008). This is especially important when modeling a generalist large carnivore that is expanding into its historic range.

The program ENM Tools was then used to calculate the Akaike Information Criterion corrected for small sample size (AICc) and AICc model weights for each MCP and kernel model (ENM Tools version 1.3; Warren et al. 2010). For both methods the model with the lowest AICc indicated the importance of the same variables in pack habitat suitability. Therefore, MCPs were determined to be sufficient for region wide habitat analysis. MCP-identified random location points were therefore used across the entire study area for all further pack habitat suitability analyses.

Every combination of variables was then run in Maxent for both MCP-identified random pack locations and dispersal GPS locations. This resulted in the formation of 26 possible habitat suitability models for both wolf packs and dispersing wolves. ENM Tools was then used to calculate the AICc value for all Maxent habitat suitability models created for packs and dispersers. The models with the lowest AICc were selected as the top models and used for all future analyses. Relative variable importance within the model was also determined using Maxent's percent contribution and permutation importance calculations. Percent contribution was measured by the increase in regularized gain for each iteration of the training algorithm. Permutation importance was estimated for each variable by randomly permutating the value of that variable on the training and background data for the final model only.

Least Cost Path Connectivity

I then exported the top suitability model as a raster file into the geospatial analysis program ArcMap 10.1 for the purpose of conducting a connectivity analysis, as well as providing a more visually appealing model presentation (LaRue and Nielsen 2008). All connectivity analyses utilized the identified disperser habitat suitability model, as this more accurately described how wolves chose to move while dispersing. Connectivity modeling was performed using the Spatial Analyst toolbox in ArcMap 10.1. A cost surface was created by assuming the inverse of the disperser habitat suitability model was an estimate of a least cost path following Huck et al. (2011). Dispersal barriers such as rivers, lakes, and extreme slopes were not included. Wolves are known to be very good swimmers and have been observed swimming up to 4 km (Person and Ingle 1995; Darimont and Paquet 2002). Due to the pixel resolution of 1 km, slope was not able to identify areas of steep enough slope to act as a barrier to wolf movement. In Washington, least cost paths were calculated between the fragmented habitats of highest quality within areas of interest in Washington as determined by the Washington Department of Fish and Wildlife: eastern Washington, the northern Cascades, the southern Cascades and the northwest coast (Becker et al. 2013). Due to clumping of high quality habitat, the western coast of Washington was separated into the Olympic peninsula and southwestern Washington. This same method was utilized for Oregon, determining least cost paths between northeastern Oregon, northern Cascades, central Cascades, Siskiyou Mountains, northern coast, central coast, and southern Coast. High quality habitats were determined as areas with identified habitat suitability value greater than 0.5 in Washington and

Oregon based on the pack Maxent model (Mladenoff et al. 1995). Due to a lack of habitat meeting these same standards in California, high quality habitat in that state was identified as that with a habitat suitability value greater than 0.4. In California, connectivity was tested between Northern Central California and the Northern Sierras from the likely immigration source of the Southern Oregon coast and the Siskiyou Mountains. All least cost paths were buffered by 1 km to more accurately depict a useful potential dispersal corridor.

RESULTS

Comparison of Kernel Density and MCP Home Ranges

To ensure that MCP home range estimation only was appropriate for this study, MCP and fixed kernel home range estimation methods were compared using Washington data. After modeling predicted habitat use for both methods using actual GPS collar location in Washington State, models were created for every combination of variables (Table 2). Both the minimum convex polygon and fixed kernel methods resulted in the creation of very similar models, based on AICc values. The Akaike model weight values also identified a single top model for both the minimum convex polygon and fixed kernel methods. The top model in both cases were found to have a weight of 1, indicating that they had an extremely high probability of being the model that best described wolf pack habitat use out of the models tested (Wagenmakers and Farrell 2004).

The top model created using both the minimum convex polygon and the fixed kernel method included the ungulate index and land cover type; the next top model included the ungulate index and the human footprint (Table 2). Based on model similarity, MCP home range determination was considered appropriate, and random MCP location points were used exclusively in all following wolf pack modeling analyses.

Table 2. Model selection for all model combinations, describing habitat suitability of packs identified using the MCP and fixed kernel methods for gray wolves in Washington State only. Models are ordered from lowest to highest AICc value.

	Minimum Convex Polygon				Fixed Kernel			
Model	Parameters	AICc score	Δ_i AICc	w_i AICc	Parameters	AICc score	Δ_i AICc	w_i AICc
Ungulates + Land cover	21	188944	0	1	22	241748	0	1
Ungulates + Human Footprint	35	194693	5750	0	26	258600	16851	0
Ungulates + Land cover + Human Footprint	26	209054	20110	0	28	264144	22396	0
Ungulates + Slope + Land cover	24	218819	29876	0	28	281366	39618	0
Ungulates + Slope	27	222673	33729	0	29	285285	43536	0
Human Footprint + Land cover	17	228792	39848	0	20	291475	49727	0
Land cover + Human Footprint + Slope	26	233887	44943	0	27	298982	57233	0
Land cover + Slope	22	239090	50147	0	32	303068	61319	0
Human Footprint + Slope	32	244874	55930	0	45	312741	70993	0

Pack Habitat Suitability

Using all MCP-identified home ranges, a habitat suitability model was created for wolf packs in the Pacific Northwest. The model created for all wolf packs combined resulted in a best model that included the ungulate index, land cover type, and slope, as compared to the next top model which included the ungulate index and slope only (Table 3). All models including the ungulate index performed better than any model without this variable.

The ungulate index was found to have a 77.3% contribution while land cover and slope contributed 13.4 and 9.3%, respectively, reported by Maxent when measured by regularized gain (Table 4). These variables also had a 74.2, 16.6, and 9.2 permutation contribution, respectively, based on jackknife runs on randomly permutated background points (Table 4).

Variable response curves indicated that wolves in packs generally inhabited areas of varying prey availability ranging primarily between an index value of 0.5 and 1.5 ungulates per km^2 (Figure 3). Model replication identified high precision until approximately an index value of 2, where one standard deviation included approximately 0.1 probability of presence. Wolves were shown to preferentially use forested land cover types, such as mixed forest and woodland, while avoiding more open and disturbed land cover types such as grassland and cropland (Figure 4). More open land cover types such as open shrubland and grassland were selected less frequently and anthropogenic land cover such as crop land and urban areas were even less likely to contain a wolf pack. Model replication showed precision was relatively constant across the range of land cover

Table 3. All model combinations for describing habitat suitability of packs identified using the MCP method, for gray wolves in the entire Pacific Northwest study area. Models are ordered from lowest to highest AICc value corresponding to best to worst predictive model.

Model	Parameters	AICc score	Δ_i (AICc)	w_i (AICc)
Ungulates + Slope + Land cover	20	9109	0	1
Ungulates + Slope	11	9136	27	0
Ungulates + Land cover + Human Footprint	20	9145	36	0
Ungulates + Land cover	16	9206	97	0
Ungulates + Human Footprint	14	9220	110	0
Human Footprint + Land cover + Slope	16	9496	387	0
Land cover + Slope	10	9557	448	0
Land cover + Human Footprint	10	9583	473	0
Human Footprint + Slope	17	9613	504	0

Table 4. Maxent generated estimates of relative percent contribution and permutation importance for each of the three variables identified in the top pack model.

Variable	Percent Contribution	Permutation Importance
Ungulates	77.3	74.2
Slope	13.4	16.6
Land Cover	9.3	9.2

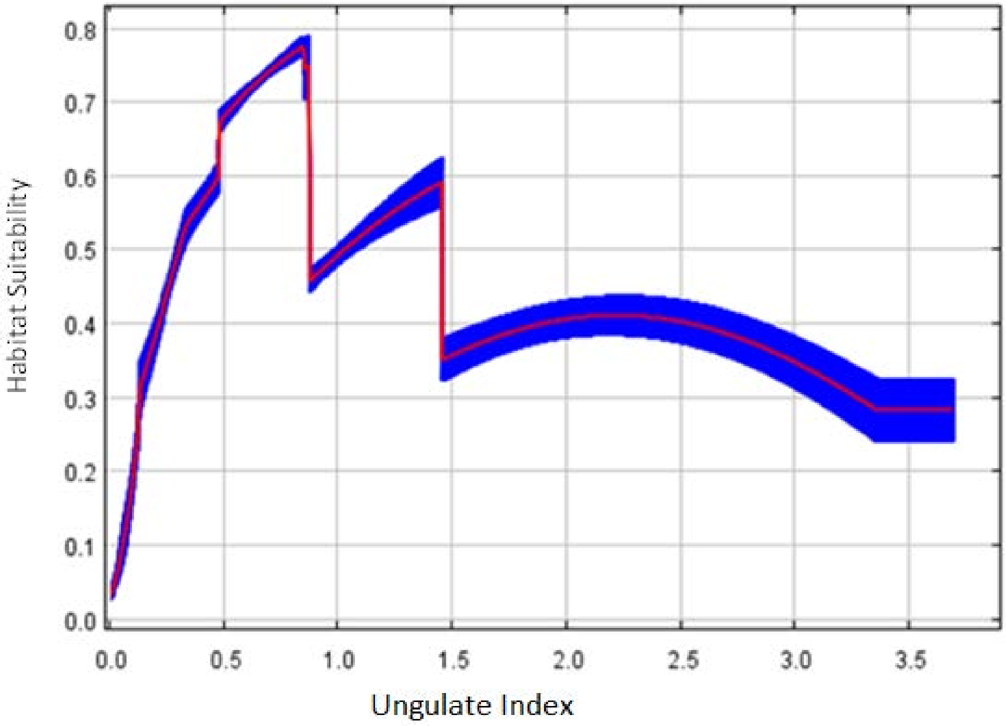


Figure 3. Maxent-generated response curves of wolf pack habitat suitability for the ungulate index variable identified in the top pack model. The red line indicates the Maxent-derived probability of presence compared to the value of the variable. Blue shading represents the error associated with a single standard deviation after five model replicates.

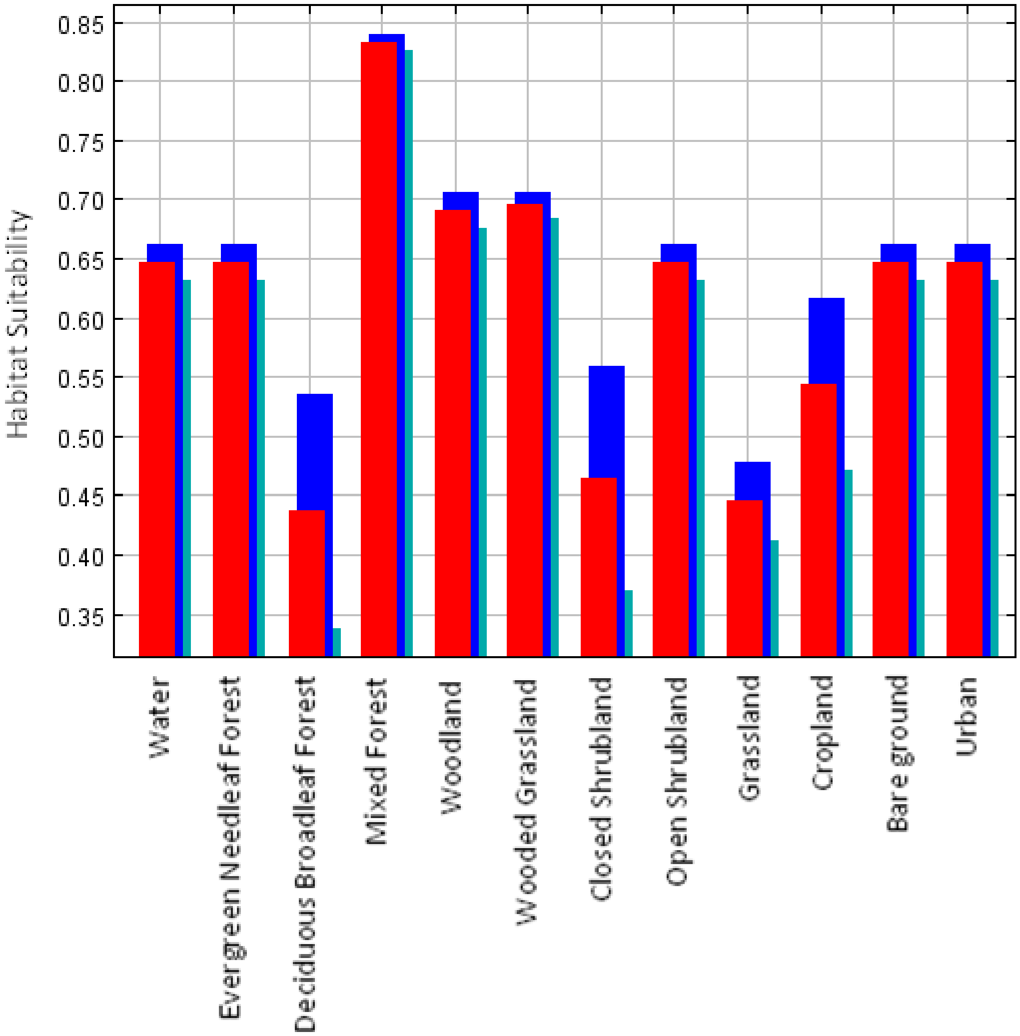


Figure 4. Maxent-generated response of wolf pack habitat suitability for the land cover variable identified in the top pack model. The red bar indicates the Maxent-derived probability of presence compared to the value of the variable. Blue and green shading represent the error associated with a single positive and negative standard deviation respectively, after five model replicates.

types and never exceeded 0.1 probability of presence (Figure 4). Areas of relatively high landscape-level slope were more likely to contain a wolf pack than less gentle-sloping areas (Figure 5). Standard deviation in slope was consistently relatively low, never exceeding 0.1 probability of presence within one standard deviation. Overall cross validation evaluation of the wolf pack model resulted in low deviation between model iterations, indicating high model stability and predictive performance (Elith et al. 2011).

Highly suitable habitat was identified for wolf packs in Washington, Oregon and California (Figure 6). Primarily highly suitable habitat for Washington was located in the Northeast, Southwest, and Southeast corners of the state, along with the Olympic peninsula. Areas of low habitat suitability were found in the Northwest and Southeast portions of the states, excluding a small portion of the Southeast corner. Oregon contained the most highly suitable habitat with highest quality habitat in the Northeast and Western portions of the state. Areas identified as low quality habitat included the high desert portions of the state including the Southeast and along the eastern edge of the cascades as well as the Willamette Valley immediately south of Portland. California was shown to have the least amount of highly suitable habitat. In California, areas of high habitat quality were concentrated in the Northeast of the state as well as the Northern Sierra Nevada Mountains (Figure 6).

Disperser Habitat Suitability

Using GPS locations for all individual dispersing wolves (n=15), a habitat suitability model was created for dispersers in the Pacific Northwest. The best model

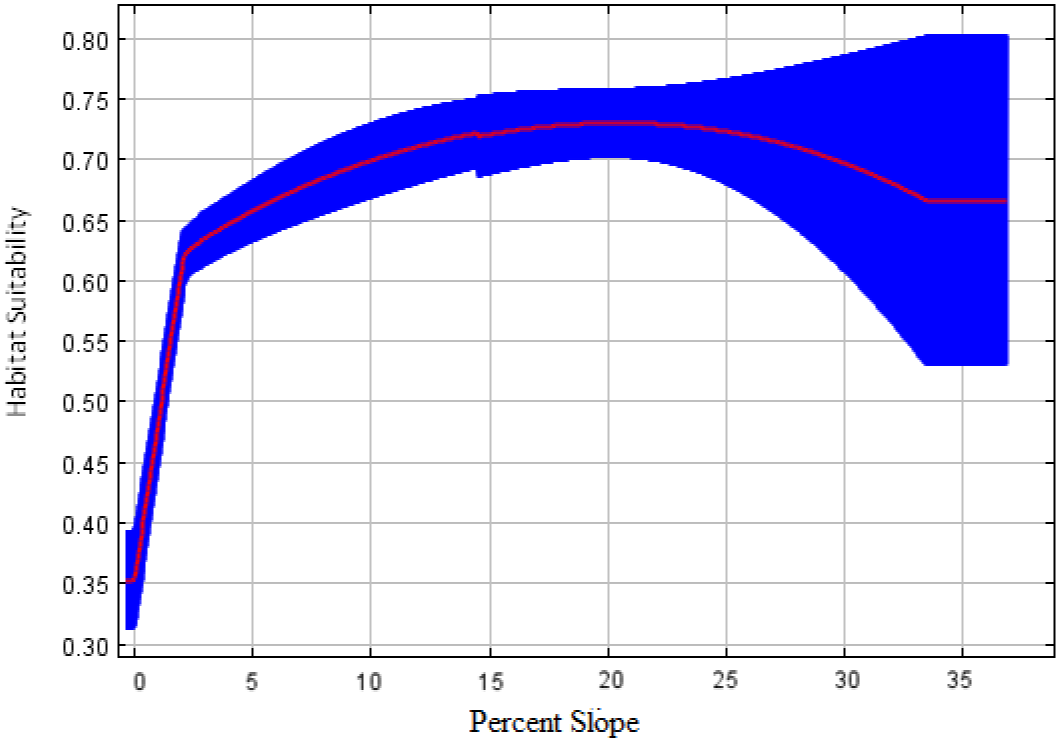


Figure 5. Maxent-generated response curves for the slope variable identified in the top pack model. The red line indicates the Maxent-derived habitat suitability compared to the value of the variable. Blue shading represents the error associated with a single standard deviation after five model replicates.

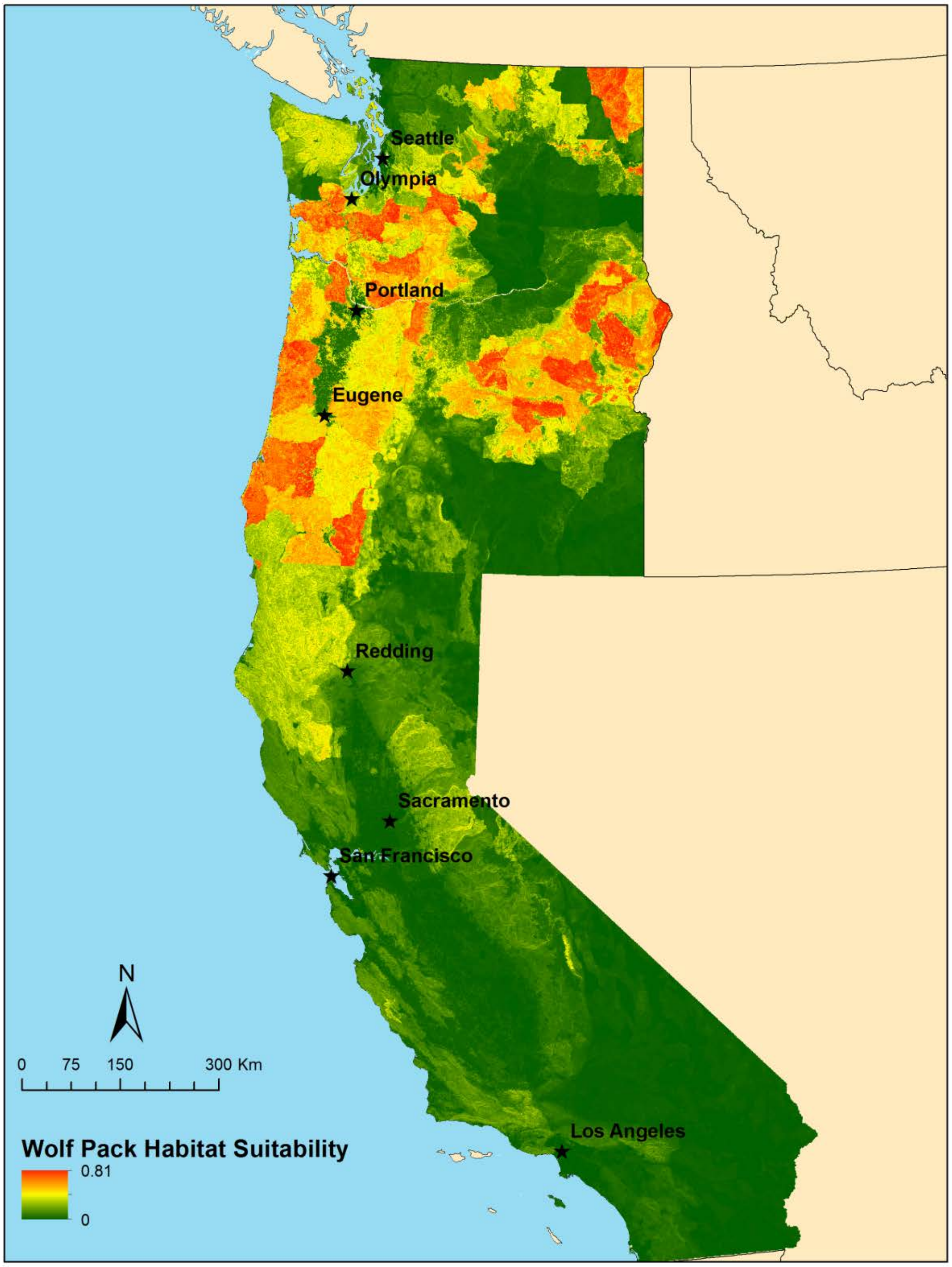


Figure 6. Maxent-generated habitat suitability map for gray wolf packs in the Pacific Northwest. Green indicates areas of lowest suitability and red indicates areas of highest suitability. Map projected using NAD 83 UTM zone 11N.

included the ungulate index and human footprint, while the next top model included the ungulate index and land cover (Table 5).

Models including the ungulate index variable all had AICc values lower than any model without it (Table 5). However, the human footprint variable was included in the top model, while land cover was not. Slope was also not included in the top three models unlike the pack model. The ungulate index variable was found to have an 85.1% contribution while human footprint had a 14.9% contribution as measured by the regularized gain in Maxent (Table 6). These variables also had an 88.2 and 11.8 permutation contribution respectively based on a jackknife run on randomly permutated background points (Table 6).

Response curves indicated that dispersing wolves generally traveled through areas of varying prey availability primarily ranging from approximately between 0.5 and 1.2 ungulates per km^2 (Figure 7). Dispersing wolves were shown to primarily select habitat with a human footprint roughly between 10 and 20 out of a scale to 100 (Figure 8). Standard deviation testing showed very little variation between replicates and overall less variation compared to the wolf pack model. Overall cross validation evaluation of the wolf pack model indicated low error and relatively high predictive performance.

Highly suitable habitat was identified for dispersing wolves in Washington, Oregon and California (Figure 9). Primarily highly suitable habitat in Washington for dispersers was identified at a much smaller scale than for packs. Suitable dispersal habitat was interspersed throughout the state including areas in the Northeast, Southwest, Central, and Southeast corner of the state. Disperser habitat suitability was high

Table 5. All model combinations for describing habitat suitability of dispersing wolves in the Pacific Northwest study area. Models are ordered from lowest to highest AICc value corresponding to best to worst predictive model.

Model	Parameters	AICc score	Δ_i (AICc)	w_i (AICc)
Ungulates + Human Footprint	31	199966	0	1
Ungulates + Land cover	27	200696	730	0
Ungulates + Land cover + Human Footprint	39	201911	1946	0
Ungulates + Slope + Human Footprint	41	205176	5210	0
Ungulates + Slope + Land cover	47	205533	5568	0
Ungulates + Slope	25	206053	6087	0
Land cover + Human Footprint	20	209398	9432	0
Land cover + Slope + Human Footprint	29	210386	10421	0
Slope + Land cover	22	211707	11741	0

Table 6. Maxent-generated estimates of relative percent contribution and permutation importance for each of the variables identified in the top disperser model.

Variable	Percent Contribution	Permutation Importance
Ungulates	85.1	88.2
Human Footprint	14.9	11.8

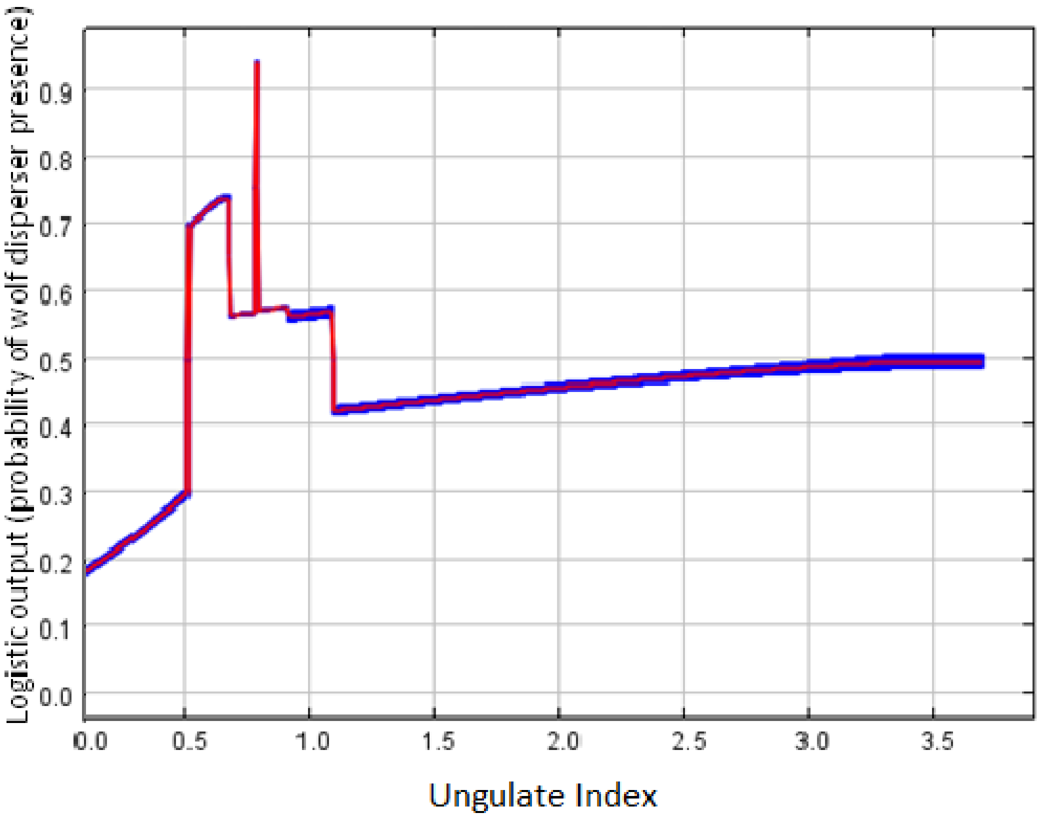


Figure 7. Maxent-generated response curves for the ungulate index variable identified in the top disperser model. The red line indicates the Maxent-derived habitat suitability compared to the value of the variable. Blue shading represents the error associated with a single standard deviation after five model replicates.

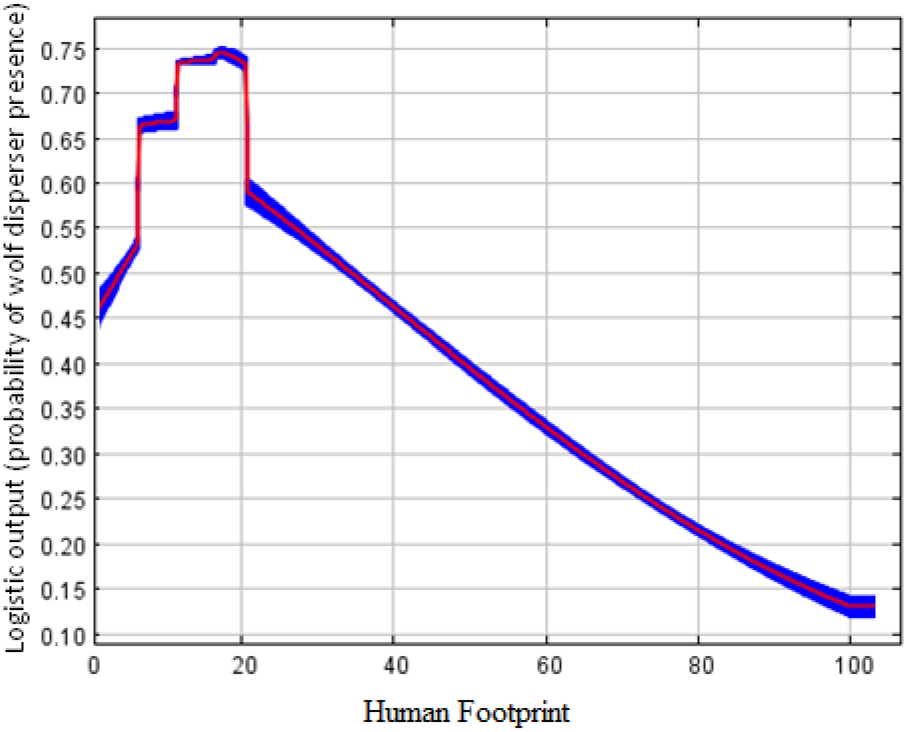


Figure 8. Maxent-generated response curves for the human footprint variable identified in the top disperser model. The red line indicates the Maxent-derived habitat suitability compared to the value of the variable. Blue shading represents the error associated with a single standard deviation after five model replicates.

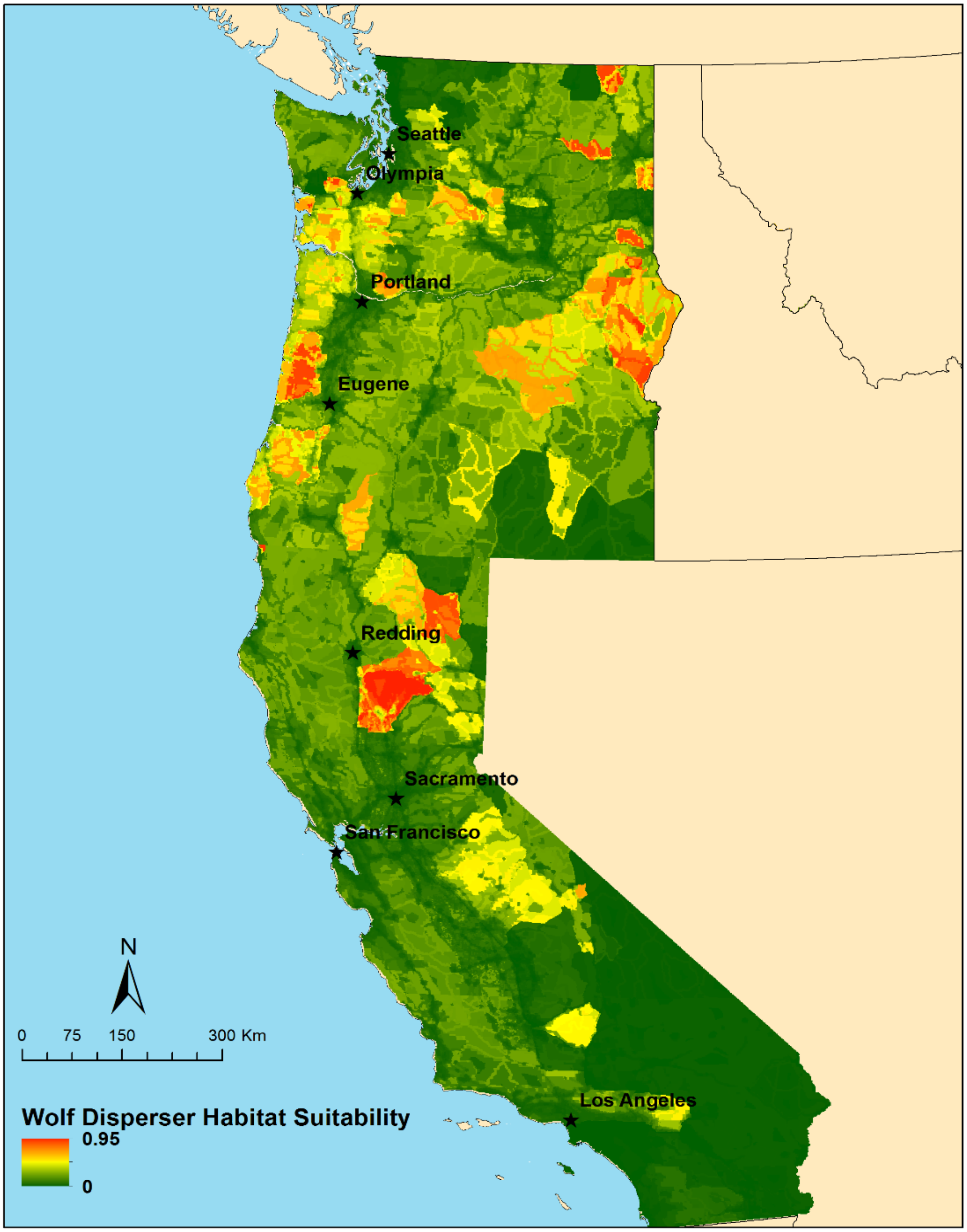


Figure 9. Maxent-generated habitat suitability map of gray wolf dispersers in the Pacific Northwest. Map projected using NAD 83 UTM zone 11N.

surrounding the Olympic peninsula but low within the Olympic National Park itself. Areas of low habitat suitability were concentrated primarily in the Northwest and the Columbia Basin Plateau. Disperser habitat quality was also much lower surrounding the urbanized areas of the state, most noticeably surrounding Seattle. Oregon's highest quality habitat for wolf dispersers was found in the Northeast and Western portions of the state. Areas identified as low quality habitat were similar to the pack model and included the high desert portions of the state in the Southeast and along the eastern edge of the cascades, along with the Willamette Valley and other highly populated areas. California was shown to have more highly suitable habitat for dispersers than for packs. Areas of high habitat quality were concentrated primarily in the Northern Sierra Nevada Mountains. In all regions patterns of suitable habitat following roadways was observed.

Least Cost Path Connectivity

Least cost path analysis identified six possible corridors between highly suitable habitat patches in Washington State, using the inverse of the disperser habitat suitability model (Figure 10). Two dispersal paths emanating from Northeast Washington followed similar routes for a portion of the distance to their destinations patches of the Northern and Southern Cascades. These two routes originated in the Spokane Indian Reservation and followed the southern bank of the Columbia River until they split near Grand Coulee, Washington. The northern cascade route then turned north where it crossed the Columbia River at a narrow portion and continued to the Okanagan National Forest just north of Omak, Washington. The southern Cascade route continued west across high desert and agricultural land until it crossed the Columbia River near Trinidad, Washington and

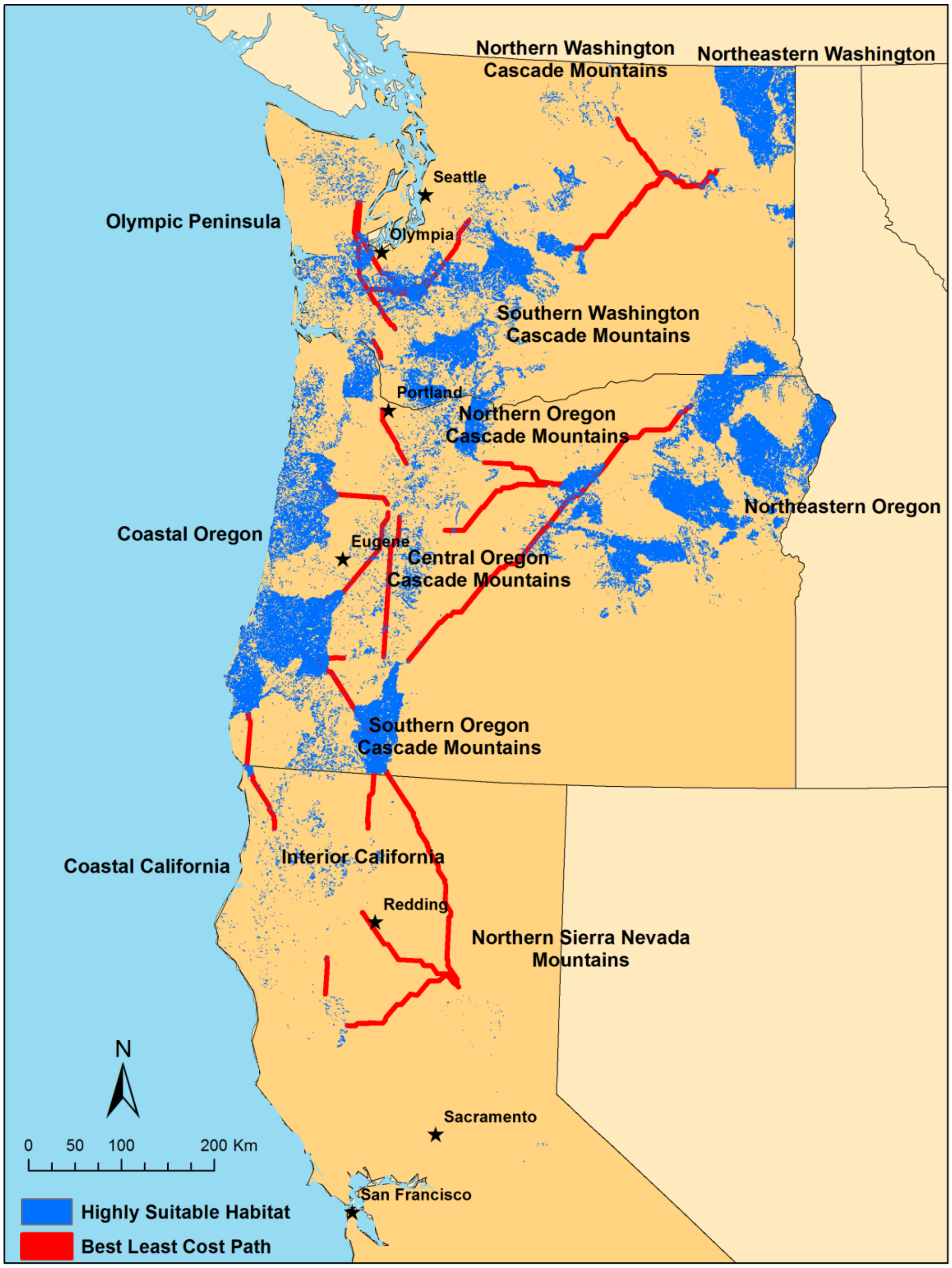


Figure 10. Least cost path analysis indicating possible dispersal corridors for gray wolves between patches of highly suitable habitat. Map projected using NAD 83 UTM zone 11N.

terminated in the mountains just west of the river. This latter dispersal route was the longest of those calculated in Washington and totaled approximately 388 km.

The southern Cascade Mountains were identified as having a large amount of highly suitable habitat across their entirety, while the northern Cascades had much less suitable habitat concentrated primarily on the eastern slopes (Figure 10). Paths were calculated from both of these regions to the Olympic peninsula as well as southwestern Washington. All paths avoided the major urban area surrounding Seattle, but both paths to the Olympic Peninsula crossed through the relatively small city of Olympia. The paths to the southwest portion of the state also intersected areas of low density human habitation near Chehalis and North of Kelso, Washington as well as crossing the four lane Interstate 5 highway.

In northeastern Oregon, the paths calculated to the northern and central Cascades and the Siskiyou Mountains all began in the Umatilla Indian Reservation and moved along the northern edge of the Umatilla forest (Figure 10). At the end of the forest, the paths diverge with the northern path traveling into the Warm Springs Indian Reservation. The central Cascade path crossed into the Cascades near Madras, Oregon ending its path in the Deschutes National Forest. Dispersal corridors between the Cascades on available habitat on the western Oregon coast were predicted to circumnavigate the Willamette valley except for wolves in the central Cascades. This least cost path predicted movement of wolves across the relatively less urbanized portion between Salem and Albany. In the northern Cascades, wolves were predicted to move across the suburban area south of Portland and into Portland’s Forest Park. The paths originating from the central Cascades and the Siskiyou Mountains traveling to the south coast predicted a corridor for movement into the coast range near Cottage Grove, Oregon.

In California, least cost paths were calculated originating on the southern coast and the Siskiyou Mountains of Oregon and traveling to the Klamath Mountains in the northern interior and the northern Sierra Nevada Mountains. Along the coastal portion of the state, a least cost path predicted movement through the Siskiyou National Forest southward into the Six Rivers National Forest in California. This path skirted the western edge of the National Forests until moving inland just east of Redwood National and State Parks and into high quality habitat in the Six Rivers and Shasta-Trinity National Forests. Further, a path was identified connecting the northern Sierras to the Oregon Siskiyou Mountains and traveling along the eastern slopes of Mount Shasta and into the Lassen National Forest. Similarly the interior California habitat was connected to the Lassen National Forest with paths traveling through the Sacramento valley and crossing the Sacramento River near highly agricultural areas surrounding Redding and Chico California.

DISCUSSION

Habitat Models

Prior research has been conducted on the habitat requirements of wolves, however, no modeling of wolf habitat has been conducting in the Pacific Northwest using empirical data. For the first time wolves were separated based on behavioral differences between dispersing and pack individuals. This distinction allowed us to predict areas of potential future wolf dispersal in the expanding Pacific Northwest population. Identification of potential dispersal pathways also allowed for a more accurate prediction of future wolf movements.

Habitat use by gray wolves in the Pacific Northwest appears to be primarily driven by four factors. The factor identified in all models as the most influential in use was the ungulate index variable. This variable was present in the best pack and disperser models and contributed the greatest predictive power. This was expected based on previous studies in neighboring regions, as well as from the generalist nature of wolves. Wolves are able to exist wherever prey is present, and conflict with humans is limited such that wolves are allowed to persist on the landscape (Mech and Boitani 2007). Due to the overwhelming impact of a single variable it is important to use “simple models” with few predictors as new variables likely add relatively little explanatory inference while increasing uncertainty and leading to over fitting of data. The Pacific Northwest population of wolves is particularly prone to model over-fitting as unused areas may not be considered selected against, as wolves have only recently become reestablished in the region (Carroll et al. 2003). Also, due to inherent error in 1-km resolution data it is important not to over fit the data, as this will lead to improper conclusions about habitat requirements. This limitation in resolution also requires that model results be considered only at large spatial scales.

The ungulate density index may also be considered a limitation of this study. It cannot be considered to be a true surrogate for ungulate density, which is likely to be closer to the environmental cue that wolves use to select habitat. Total harvest is determined by a number of factors including ungulate population numbers, desired management objectives, hunter accessibility, etc. However, due to the scale of this study and the inconsistency of ungulate population estimates across the study area, the ungulate index was considered the best indicator of relative ungulate abundance. Future research should be conducted as more accurate ungulate density estimates become available.

Land cover type was another factor influencing wolf pack habitat use. This environmental variable has also been identified as an important indicator of wolf habitat use in previous studies (Mladenoff et al. 1995; Oakleaf et al. 2006). As land cover type relates greatly with the ability of wolves to find and successfully hunt prey items, this is to be expected. Wolves tended to occur predominantly in higher forest cover land types. This is partially influenced by wolf habitat selection based on prey density, as ungulates also tend to inhabit areas with access to higher vegetative cover (Wydeven and Dahlgren 1985; Mysterud and Ostbye 1999). Furthermore, wolf hunting success is higher in areas of high cover compared to low cover during summer months due to decreased maneuverability of ungulates in forested areas (Edge et al. 1987). This variable is also able to address the relationship between wolf and human space use in a different way than the human footprint variable, as it more directly reflects the actual cues that the wolf uses to select habitat, rather than human population density, which a wolf likely is unable to access.

Use of areas with relatively higher slope was observed to be a significant driver of wolf pack habitat selection, likely due to prey foraging behavior and wolf movement cost while hunting. In winter months, ungulates have been observed to prefer areas of moderate to high slope due to a decreased snow pack on steeper hillsides (McCorquodale 2003). Movement through areas of reduced snow pack along steep slopes is thought to decrease predation risk due to increased mobility (McCorquodale 2003). This allows ungulates to graze in areas that would otherwise be under significantly more snow in winter months, thus reducing their energetic cost to forage (Arjo and Peltscher 2004). The same concept also holds for wolves which use low snow pack and reduced vegetation areas for travel within the territory (Kunkel and Pletscher 2001). In Yellowstone National Park, migrating pronghorn (*Antilocapra americana*) were observed selecting areas of high elevation and high slope after the reintroduction of wolves (Barnowe-Meyer et al. 2010). Observations of elk foraging habitat have indicated a decreased use of low-lying meadows and riparian areas in possible response to wolf presence (Ripple and Betscha 2004). This behavioral adaptation to the presence of wolves can result in high-elevation ungulate refugia where prey concentrate (Barnowe-Meyer et al. 2010). Steep terrain may reduce wolf hunting success rates due to increased prey maneuverability and ability to spot incoming predators for some ungulates on steep terrain (Kie 1999; Risenhoover and Bailey 1985). Despite a possible reduction in efficiency at high slope, wolf kills occur most often in areas of the lowest snow depth primarily due to a concentration of prey in these areas (Kunkel and Pletscher 2001). It is due to this seasonal variation in prey behavior that requires wolf territories to contain both highly forested areas (as described by the land cover type variable), as well as steep slopes with reduced snow pack and vegetative cover.

The change of behavior of ungulate prey species in the presence of wolves may contribute to the observation that dispersing individuals did not appear to select habitat based on slope. Slope was not included in any of the top three disperser habitat selection models. This is possibly due to the historic lack of wolves in non-inhabited areas. That is, in areas where wolves have been extirpated and no new wolf packs have yet been established, prey are more likely to congregate in lower elevation, less steep areas, as predation risk has historically been low and forage quality is higher in these low lying areas (Festa-Bianchet 1998; Ripple and Betscha 2004; Creel et al. 2005). In addition, the directional tendency of long distance dispersers likely reduces the ability of dispersing wolves to select for slope. As dispersing wolves appear to be able to cross relatively poor habitat, optimal areas for hunting are not being selected for during actual dispersal. Long distance dispersing wolves find success when they obtain a mate and territory (Mech and Boitani 2007).

Research suggests that gray wolves are able to travel through habitat considered as poor in the search for an area to form a new pack (Mech et al. 1995; Merrill and Mech 2000). It is for this reason that selection must be considered at the individual disperser level when predicting possible dispersal corridors. This may explain why dispersing wolves selected for areas with low to moderate levels of anthropogenic activity. By visually comparing dispersing wolf location points to the human footprint layer it is apparent that dispersing wolves remain closer to higher human density areas and utilize roads more often than wolves in packs. Utilization of human roadways decreases long distance movement costs as well as provides a possible food source through road kill, likely facilitating the directional dispersal observed in wolves. However, utilization of roadways increases the risk of vehicle-related mortality and interaction with humans.

Areas of Predicted Wolf Expansion

Currently the majority of wolf packs within Washington state are located in the Northeastern corner and the Northern Cascade Mountains. Although this habitat is clearly suitable for wolves, the highest quality habitat to the southwest remains uninhabited. Northern Yakima County and areas surrounding Mount Rainier National Park were identified as areas with very high pack suitability, while their proximity to the currently established Teanaway and Wenatchee packs suggests high probability of wolf expansion into this region. Least cost path corridors indicated a high quality corridor between these high quality areas surrounding Mount Rainier to the Coastal mountain ranges. In particular, several least cost paths connected high quality habitat patches through southeastern Grays Harbor County, northeastern Lewis County, and southwestern Thurston County, in the northwest of the state (Appendix A). The intersection of Thurston, Lewis, and Grays Harbor Counties has been identified as an area of likely wolf activity based on habitat quality and connectivity to other patches of high quality habitat.

This region was shown to be an area wolves may pass through if dispersal were to occur to the Olympic peninsula. Due to its high habitat suitability and highly connected nature, this is an area that requires consideration for future gray wolf management and conservation measures. The Olympic peninsula was not identified as an area of high habitat suitability primarily due to an underestimation of ungulate density due to lack of harvest data in the large national park. This lack of data also contributes to a low estimated habitat suitability of the Northern Cascades National Park.

In Oregon, several regions were identified as areas for focusing wolf monitoring and future conservation efforts. Wheeler County, in central Oregon, was found to be particularly high quality wolf habitat as well as having all calculated least cost path corridors from the highly wolf dense northeast passing through it. Wheeler County, specifically the Umatilla National Forest, is a prime location for wolf dispersal and expansion. Based on this, I suggest focusing observational effort for dispersing wolves in this area. Highly suitable habitat was also indicated surrounding Mount Hood on the eastern slopes of the Oregon Cascades. This along with proximity to bordering high quality habitat in Washington, may be an area of likely wolf expansion. Also, due to its high wolf pack suitability, Coos County and western Douglas County to the southwest have been identified as areas of likely wolf expansion. The establishment of the Rogue wolf pack in 2014 in this region further supports this finding.

Least cost paths from the central Cascades identified potential areas of conflict between wolves and humans. Corridors connecting high quality habitat were identified to pass through southern Portland suburbs despite very high human population density in this region. Due to the urbanized nature of this area, risk of conflict is greatly increased. Also due to the path’s relative proximity to high quality habitat to the west as well as to the east near Mount Hood, it is possible that in the future, action may need to be taken to facilitate wolf dispersal around these areas or even to discourage movement across this region. Further south, wolves were predicted to move across the Willamette valley despite its low suitability. This region is substantially less urbanized, but high agricultural land use may also lead to conflict if wolves were to disperse through this area.

There was less high quality habitat identified in California as compared to Oregon or Washington. This is likely due to the use of an ungulate density index based on total deer and elk harvest. The California Department of Fish and Wildlife estimates that there were 443,289 total deer in the state and 14,733 (0.03%) were reported killed by hunters in 2013 (CDFW 2014). This is in contrast to Washington in which there were an estimated 300,000 to 320,000 deer and 33,657 (~10%) deer hunted in 2013 (WDFW 2014). In Oregon in 2012, 43,098 (~9%) deer were reported hunted out of ~500,000 as of 2009 (ODFW 2013). These data suggest that despite an estimated greater deer population, a much lower percentage of deer were hunted in California. For this reason much of the habitat is likely of higher quality to wolves than indicated in this study.

Areas of highest habitat quality in California were identified in the northern interior and northern Sierra Nevada Mountains. High quality habitat and proximity to the established Rogue wolf pack of Oregon indicate that the Six Rivers and Shasta-Trinity National Forests are areas of probable wolf expansion. Lassen National Forest was also identified as highly suitable habitat for wolf packs and is the ending location of all surrounding dispersal corridors. High quality habitat was also identified further south in the Tahoe National Forest. Additionally, a dispersing wolf from Oregon spent over a year in this region on a dispersal foray, indicating wolf establishment in this region is likely. Although humans do inhabit habitat identified as high quality these are relatively low population areas. Within California it appears that wolves have high enough quality habitat and low enough risk of conflict with humans that they will likely be able to reestablish a population within the northern portion of this state.

Throughout the study area the formation of several new confirmed wolf packs not available for use in this study lend support for the identification of habitat quality by this study. In particular the Huckleberry, Dirty Shirt, and Carpenter Ridge packs in Washington were recently formed in areas identified in this study as high quality and high connectivity, and were therefore predicted to have a high probability of pack formation. Similarly in Oregon, habitat and connectivity were considered high in the area where the newly observed Keno Pair have been identified. Additionally, reports of the Desolation wolves located in Northeastern Grant County occur in an area considered highly suitable for packs as well as highly connected.

Gray wolf expansion has been a contentious issue within the United States for decades. As protected gray wolves disperse into new areas, state agencies will be required to alter their management strategies to meet not only the needs of wolves but also those of surrounding human populations. This study intended to help inform these agencies as to which areas are most likely to be inhabited by wolves in future years, as well as through which areas they may travel to reach new territories. An understanding of the variables that influence wolf movements and habitat selection during different life stages is essential for future planning, allowing managers to shape their decisions to improve conservation efforts of an endangered species while at the same time reducing conflict with humans. It is by this inclusion of human and wildlife conservation goals that we may continue to coexist with these and other large carnivores that were once ubiquitous across the landscape of the United States.

LITERATURE CITED

Arjo, W. M., and D. H. Pletscher. 2004. Coyote and wolf habitat use in northwestern Montana. Northwest Science 78:24-32.

Bangs, E. E., S. H. Fritts, J. A. Fontaine, D. W. Smith, K. M. Murphy, C. M. Mack, and C. C. Niemeyer. 1998. Status of gray wolf restoration in Montana, Idaho, and Wyoming. Wildlife Society Bulletin 26:785–798.

Barnowe-Meyer, K. K., P. J. White, T. L. Davis, D. W. Smith, R. L. Crabtree, and J. A. Byers. 2010. Influences of wolves and high-elevation dispersion on reproductive success of pronghorn (Antilocapra americana). Journal of Mammalogy 91:712-721.

Becker, S. A., P. F. Frame, D. Martorello, and E. Krausz. 2013. Washington Gray Wolf Conservation and Management 2012 Annual Report. Pages WA-1 to WA-16 in U.S. Fish and Wildlife Service Rocky Mountain Wolf Program 2012 Annual Report. USFWS, Helena, Montana.

Börger, L., N. Franconi, G. D. Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393-1405.

Boyd, D. K., and D. H. Pletscher. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. The Journal of Wildlife Management 63:1094-1108.

Carbyn, L. N., S. M. Oosenbrug, and D. W. Anions. 1993. Wolves, bison and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. Canadian Circumpolar Institute, Edmonton, Alberta.

Carroll, C., M. K. Phillips, N. H. Shumaker, and D. W. Smith. 2003. Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic spatial models. Society for Conservation Biology 17:536-548.

Carroll, C., B. H. McRae, and A. Brookes. 2011. Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. Conservation Biology 1-10.

California Department of Fish and Wildlife [CDFW]. 2014. 2013 combined deer kill info. California Department of Fish and Wildlife: Wildlife Branch Sacramento, CA.

Capitani, C., I. Bertelli, P. Varuzza, M. Scandura, and M. Apollonio. 2004. A comparative analysis of wolf (Canis lupus) diet in three different Italian ecosystems. Mammalian Biology 69:1-10.

Chavez, A. S., and E. M. Gese. 2005. Food habits of wolves in relation to livestock depredations in Northwestern Minnesota. The American Midland Naturalist 154:253-263.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387-3397.

Darimont, C. T. and P. C. Paquet. 2002. The gray wolves, Canis lupus, of British Columbias's central and north coast: distribution and conservation assessment. Canadian Field Naturalist 116:416-422.

Dudik, M., S. J. Phillips, R. E. Schapire. 2004. Performance guarantees for regularized maximum entropy density estimation. Proceedings of the 17th Annual Conference on Computational Learning Theory, ACM Press, New York, pp. 655–662.

Edge, W. D., C. L. Marcum, S. L. Olson-Edge. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. Journal of Wildlife Management 51:844-851.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151

Elith, J., S. J. Phillips, T. Hastie, M. Dudik, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43-57.

Festa-Bianchet M. 1988. Seasonal range selection in bighorn sheep: Conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75: 580–586.

Gibson, L., B. Barrett, A. Burbidge. 2007. Dealing with uncertain absences in habitat modelling: a case study of a rare ground-dwelling parrot. Diversity and Distributions 13:704-713.

Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, D. L. Mech, and R. R. Ream. 2012. Wolf population dynamics in the U.S. northern Rocky Mountains are affected by recruitment and human-caused mortality. Journal of Wildlife Management 76:108-118.

Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173-182.

Hansen, M., M. R. DeFries, J. R. G. Townshend, and R. Sohlberg. 1998. UMD global land cover classification at 1 km resolution using a decision tree classifier. International Journal of Remote Sensing. 21:1331-1365.

Hirzel, A. H., V. Helfer, and F. Metral. 2001. Assessing habitat-suitability models with a virtual species. Ecological Modeling 145:111-121.

Huck, M., W. Jędrzejewski,T. Borowik, B. Jędrzejewska, S. Nowak, and R. W. Mysłajek. 2011. Analyses of least cost paths for determining effects of habitat types on landscape permeability: wolves in Poland. Acta Theriologica 56:91-101.

Johnson, D. H., and T. A. O'Neil. 2001. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.

Kellert, S. R., M. Black, C. R. Rush, and A. J. Bath. 1995. Human culture and large carnivore conservation in North America. Conservation Biology 10:997-990.

Kie J. G. 1999. Optimal foraging and risk of predation: Effects on behavior and social structure in ungulates. Journal of Mammalogy 80: 1114–1129.

Kunkel K. E., and D. H. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management 65: 520–530.

Larsen, T., and W. J. Ripple. 2006. Modeling Gray Wolf (Canis lupus) habitat in the Pacific Northwest, U.S.A. Journal of Conservation Planning 2:17-33.

LaRue, M. A., C. K. Nielsen. 2008. Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. Ecological Modeling 212: 372-381.

Marquard-Peterson, U. 1988. Food Habits of Arctic Wolves in Greenland. Journal of Mammalogy 79:236-244.

McCorquodale, S. 2003. Sex-specific movements and habitat use by elk in the Cascade range of Washington. Journal of Wildlife Management 67:729-741.

Mech, L. D., S. H. Fritts, and D. Wagner. 1995. Minnesota wolf dispersal to Wisconsin and Michigan. American Midland Naturalist 113:368–370.

Mech, D. L. and L. Boitani. 2007. Wolves: behavior, ecology, and conservation. University Of Chicago Press, Chicago, Illinois, USA.

Merow, C., M. J. Smith, and J. A. Silander. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs matter. Ecography 36:1058-1069.

Merrill, S. B., and L. D. Mech. 2000. Details of extensive movements by Minnesota wolves (Canis lupus). American Midland Naturalist 144:428–433.

Metz M. C., D. W. Smith, J. A. Vucetich, D. R. Stahler, and R. O. Peterson. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. Journal of Animal Ecology 81:553-563.

Milakovic, B., K. L. Parker , D. D. Gustine , R. J. Lay , A. B. D. Walker , and M. P. Gillingham. 2011. Habitat selection by a focal predator (Canis lupus) in a multiprey ecosystem of the northern Rockies. Journal of Mammalogy 92:568-582

Miller, B., H. Harlow, T. Harlow, D. Biggins, and W. Ripple. 2012. Trophic cascades linking wolves (Canis lupus), coyotes (Canis latrans), and small mammals. Canadian Journal of Zoology 90:70-78.

Mladenoff D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the Northern Gray Lakes region. Conservation Biology 9:279-294.

Mladenoff, D. J., M. K. Clayton, S. D. Pratt, T. A. Sickley, and A. P. Wydeven. 2009. Change in occupied wolf habitat in the Northern Great Lakes Region. Pages 119-138 in A. P.

Morrison, M. L., B. Marcot, and V. Mannan. 2012. Wildlife-habitat relationships: concepts and applications. Island Press, Washington D.C., USA.

Musiani, M., and P. C. Paquet. The practices of wolf persecution, protection, and restoration in Canada and the Unites States. BioScience 54:50-60.

Mysterud, A., and E. Ostbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin 27:385-394.

Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A.

Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat selection by recolonizing wolves in the Northern Rocky Mountains of the United States. Journal of Wildlife Management 70:554-63.

Oregon Department of Fish and Wildlife [ODFW]. 2010. Oregon wolf conservation and management plan. Oregon Department of Fish and Wildlife, Salem, OR.

Oregon Department of Fish and Wildlife [ODFW]. 2013. 2012 expanded deer harvest estimates for individual units. Oregon Department of Fish and Wildlife, Salem, OR.

Person, D. K., and Ingle M. A. 1995. Ecology of the Alexander Archipelago wolf and responses to habitat change. Unpublished progress report 3. 39 p. On file with: Alaska Department of Fish and Game, Douglas, AK.

Peterson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102-117.

Peterson, R. O. 1975. Wolf ecology and prey relationships on Isle Royale. U. S. Government Printing Office Washington D. C.

Phillips, S. J. and M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31:161-175.

Phillips, S. J., M. Dudik, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2014. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19:181-197.

Responsive Management. 2014. Opinions on bear and wolf management and experiences with wildlife that cause problems. Responsive Management, Harrisonburg VA.

Ripple, W., E. Larsen, R. Renkin, and D. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227-34.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766.

Risenhoover K. L., and Bailey J. A. 1985. Foraging ecology of mountain sheep: Implications for habitat management. Journal of Wildlife Management 49: 797–804.

Rutledge, L. Y., K. I. Bos, R. J. Pearce, and B. N. White. 2010. Genetic and morphometric analysis of sixteenth century Canis skull fragments: implications for historic eastern and gray wolf distribution in North America. Conservation Genetics 11:1273-1281.

Schermerhorn, V. P. 1967. Relations between topography and annual precipitation in western Oregon and Washington. Water Resources Research 3:707-711.

Singleton, P. H., W. L. Gaines, and F. Lehkuhl. 2002. Landscape permeability for large carnivores in Washington: a geographic information system weighted distance and least cost path corridor assessment. United States Forest Service Pacific Northwest Research Station. Portland, OR.

Socioeconomic Data and Applications Center [SEDAC]. 2005. Global Human Footprint, v2 (1995-2004). <http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic#>. Accessed 10 Dec 2014.

Stephenson, R. O. and L. J. Johnson. 1973. Wolf report. Alaska Department of Fish and Game. Juneau AK.

United States Forest Service [USFS]. 2007. Description of “ecological subregions: sections of the conterminous United States”. United States Department of Agriculture, Washington D. C.

United States Fish and Wildlife Service [USFW]. 1987. Northern Rocky Mountain wolf recovery plan. United States Fish and Wildlife Service, Denver, Colorado.

Voigt, D. R., G. B. Kolenosky, and D. H. Pimlott. 1976. Changes in summer foods of wolves in Central Ontario. The Journal of Wildlife Management 40:663-668.

Wagenmakers, E., and S. Farrell. 2004. AIC model selection using Akaike weights. Pshyconomic Bulletin and Review 11:192-196.

Waring R. H., and J. F. Franklin. 2003. Evergreen coniferous forests of the Pacific Northwest. Science 204:1380-1386.

Warren, D. L., R. E. Glor, M. Turelli. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33:607-611.

Washington Department of Fish and Wildlife [WDFW]. 2012. Grizzly bear annual report. Washington Department of Fish and Wildlife Olympia, Washington, USA.

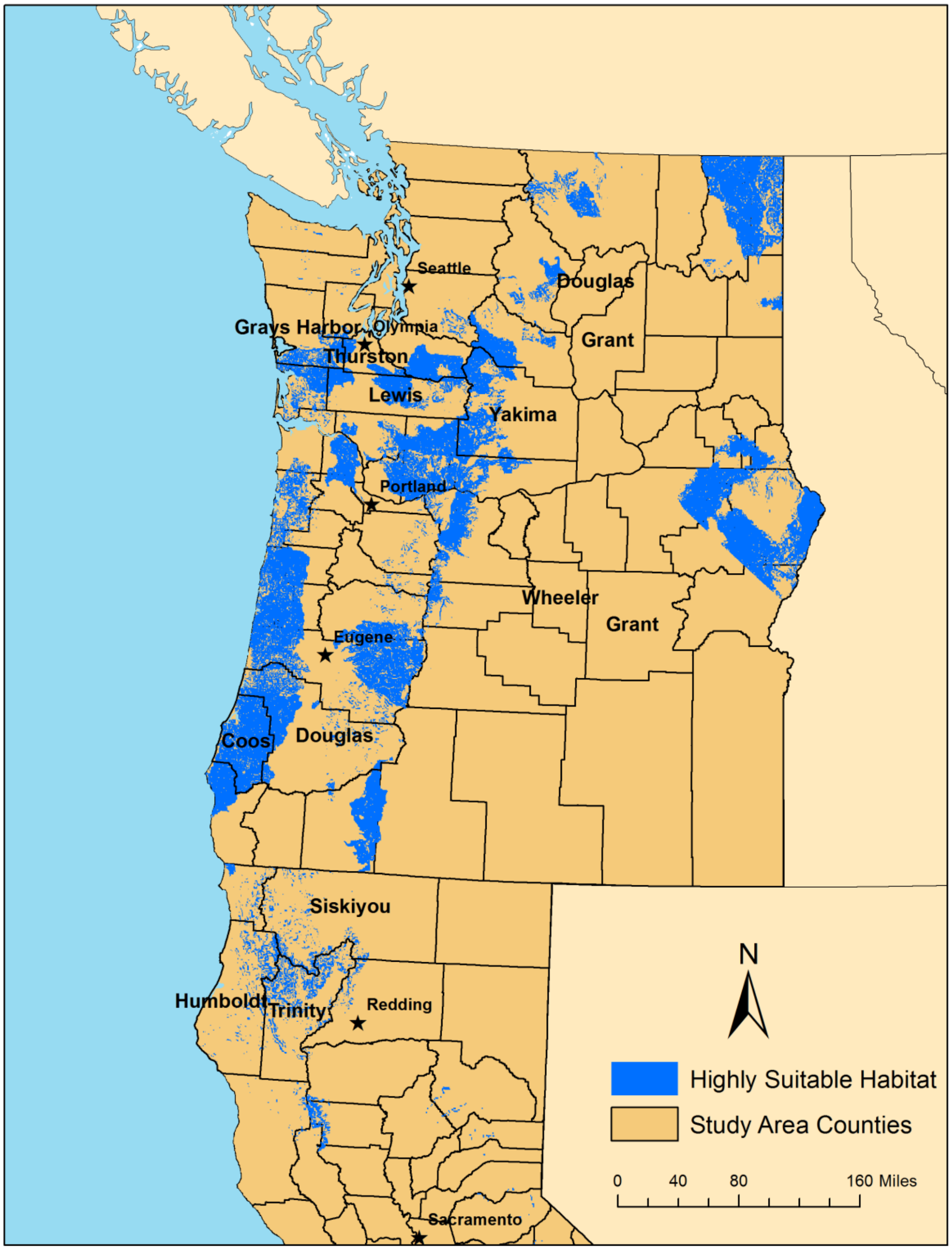
Washington Department of Fish and Wildlife [WDFW]. 2014. Washington Department of Fish & Wildlife 2015-2021 Game Management Plan. Washington Department of Fish and Wildlife Olympia, Washington, USA.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology 10:964-976.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, W. M. Getz. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72:909-916.

Wydeven, A. P., and R. B. Dahlgren. 1985. Ungulate habitat relationships in the Wind Cave National Park. The Journal of Wildlife Management 49: 805-813.

APPENDIX



Counties within the Pacific Northwest study area. Counties of identified importance to wolf expansion are labeled. Map projected using NAD 83 UTM zone 11N.